

PHYLOGENETIC STUDIES OF THE FREE-LIVING AND ARTHROPOD ASSOCIATED LAELAPIDAE (ACARI: MESOSTIGMATA)

ESTUDIO FILOGENETICO DE LAELAPIDAE DE VIDA LIBRE Y ASOCIADOS CON ARTRÓPODOS (ACARI: MESOSTIGMATA)

María E. Casanueva*

ABSTRACT

The genera of free-living and arthropod-associated Laelapidae were reviewed in an attempt to determine the internal relationships of the family. Using phylogenetic methods, with computations on the PAUP and MacClade programs, a comparative study of eighty-three characters in fifty generic taxa resulted in the construction of nine consensus cladograms illustrating familial and subfamilial relationships. The Leptolaelapidae was used as the sister group and Ologamasidae as the outgroup.

The Laelapidae was redefined to include eight subfamilies: Hypoaspidae Vitzthum, 1940; Melittiphidinae Evans and Till, 1966; Haemogamasinae Oudemans, 1926; Alphalaelapinae Tipton, 1960; Laelapinae Berlese, 1892; Myonyssinae Bregetova, 1956; Hirstionyssinae Evans and Till, 1966 and Mesolaelapinae Tenorio and Radvsky, 1974. The new arrangement of the free-living and arthropod-associated genera is the following: Family Laelapidae, with two subfamilies: Hypoaspidae, which includes the free-living, predatory and phoretic mites on Coleoptera and Blattaria, with Tribe Pseudoparasitini and Tribe Hypoaspidini, and Melittiphidinae which includes laelapid mites associates of Hymenoptera (Apidae and Formicidae) and Isoptera, with Tribe Laelaspidini, new tribe, Tribe Melittiphidini and Tribe Varroini.

The dermanyssoid mites associated with Chilopoda, Diplopoda, Araneae and crustacea are included in the famili Iphiopsididae, with two subfamilies: Scissuralaelapinae, new subfamily and Iphiopsidinae which is divided into Tribe Iphiopsidini and Tribe Gecarcinolaelapini, new tribe.

The genus *Urozercon* is included for the first time in the family Laelapidae; and the new genus *Gecarcinolaelaps* is established in Iphiopsididae. The prior ranking of *Euvarroa* and *Varroa* as the family Varroidae Delfinado and Baker, 1974 is refuted.

KEYWORDS: Acari, Mesostigmata, Laelapidae, Phylogeny.

RESUMEN

Se estudiaron los géneros de la familia Laelapidae de vida libre y asociados con artrópodos en un intento para determinar las relaciones internas de la familia. Utilizando métodos filogenéticos, con los programas PAUP y MacClade, se realizó un estudio comparativo de 83 caracteres en 50 géneros, obteniéndose nueve cladogramas de consenso que ilustran las relaciones a nivel de familia y subfamilias. Las familias Leptolaelapidae y Ologamasidae se utilizaron como el grupo hermano y grupo externo respectivamente.

Se redefine la familia Laelapidae, la cual incluye ocho subfamilias: Hypoaspidae Vitzthum, 1940; Melittiphidinae Evans y Till, 1966; Haemogamasinae Oudemans, 1926; Alphalaelapinae Tipton, 1960; Laelapinae Berlese, 1892; Myonyssinae Bregetova, 1956; Hirstionyssinae Evans y Till, 1966 y, Mesolaelapinae Tenorio y Radvsky, 1974. La posición de los géneros de la familia Laelapidae, de vida libre y asociados con artrópodos es la siguiente: a, Subfamilia Hypoaspidae que incluye los ácaros de vida libre, depredadores y foréticos en Coleoptera y Blattaria, con dos tribus: Pseudoparasitini y Hypoaspidini y, b, Subfamilia Melittiphidinae dividida en tres tribus: Laelaspidini, nueva tribu, Melittiphidini y Varroini, las cuales incluyen los laelápidos asociados a Hymenoptera (Apidae y Formicidae) e Isoptera.

Los ácaros dermanisoideos asociados con Chilopoda, Diplopoda, Araneae y Crustacea son incluidos en la

* Laboratorio de Acarología, Departamento de Zoología, Universidad de Concepción. Casilla 2407-Apartado 10, Concepción, Chile.

Familia Iphiopsididae, con dos subfamilias: Scissura-laelapinae, nueva subfamilia y, Iphiopsidinae. Esta última es dividida en dos tribus: Iphiopsidini y Gecarcinolaelapini, nueva tribu.

Se incluye por primera vez el género *Urozercon* en la

familia Laelapidae y, el género *Gecarcinolaelaps* en la familia Iphiopsididae.

PALABRAS CLAVES: Acari, Mesostigmata, Laelapidae, Filogenia.

INTRODUCTION

The dermanyssine family Laelapidae is complex, species-rich, very diverse, and very poorly understood. Hypotheses concerning the evolutionary history of this family and its relatives are minimally developed and the classification of the group is consequently inadequate. Early authors (e. g., Canestrini, Berlese) described many genera and species especially from Europe. Subsequent workers have continued with the description of new forms and, at the same time, have attempted to formulate comprehensive classifications. These efforts have failed. These mites have been placed in a single family (Vitzthum, 1943; Baker and Strandtmann, 1948) or in a number of different families (Baker and Wharton, 1952; Bregetova, 1956; Rosario, 1981). The difficulty in classification might be attributed to the wide range of anatomical forms as a result of diverse adaptation to parasitism and to the consequent concentration of studies on parasites on vertebrates while neglecting the numerous free-living and arthropod-associated species. The Laelapidae exhibits a fascinating range of habitats and associations, mostly not studied in detail.

Among the Laelapidae are many genera that developed ectoparasitic (nest-dwelling or host-dwelling) associations with mammals (35 genera), and also many free-living, soil-dwelling predatory forms (10 genera). Lesser derivative elements are soil inhabiting or nest-associated predators. The greatest anatomical and ecological diversity, however, is seen in the arthropod-associated species (43 genera). Here occur associates of Coleoptera (8 mite genera), Blattaria (2 genera), Isoptera (1 genus), Hymenoptera (21 genera), Araneae (1 genus), Myriapoda (7 genera) and terrestrial Crustacea (2 genera).

From the viewpoint of phylogenetic systematics, this family and included taxa and its relatives are not adequately characterized and understood. Can the Laelapidae be recognized as a monophyletic group (that is, can a unique evolutionary origin

be hypothesized) within a monophyletic superfamily Dermanyssoidea? The present study emphasizes the predaceous soil and arthropod-associated genera to discover major patterns of morphological variation in the lesser derivative forms and thus provide a comparative and phylogenetic basis for study of the derivative groups. Finally, comparisons with the eviphidoid family Leptolaelapidae as the hypothesized sister group (nearest evolutionary relative) and with Ologamasidae as the outgroup of Laelapidae have been done. Thus this study provides an improved classification and better understanding of the evolutionary relationships within this diverse group of Mesostigmatid mites.

MATERIAL AND METHODS

This study was based on specimens in the Acarology Laboratory at The Ohio State University, and in other museums. The total number of genera in this family is ca. 100; of this, one half is available in the collection at the Acarology Laboratory. The other half was made available by the following persons and their institutions: Dr. Torbjorn Kronestedt, Swedish Museum of Natural History, Sweden; Dr. Evert E. Lindquist, Biosystematic Research Institute, Canadian National Collection, Ottawa; Dr. David C. Lee, South Australian Museum; Dr. Marisa Castagnoli, Istituto Sperimentale per la Zoologia Agraria, Florence, Italy; Dr. George C. Eickwort, Dept. of Entomology, Cornell University; Dr. John Kethley, Field Museum of Natural History; Dr. R. L. Smiley, Smithsonian Institution, USA and Dr. Mercedes Delfinado-Baker, Beneficial Insects Laboratory, USDA.

Efforts to borrow specimens from Russia and from the Rijksmuseum van natuurlijke Historie, Leiden, Netherlands, British Museum of Natural History, England and from the Potchefstroom University Collection in South Africa were unsuccessful. As a result, I was unable to examine the following type species of genera: *Angosomaspis multisetosus* Costa, 1971; *Dynastaspis walhallae*

Costa, 1971; *Holostaspis isotricha* Kolenati, 1858; *Hypoaspis (Hypohasta) simplexans* Womersley, 1956; *Iphiolaelaps myriapoda* Womersley, 1956; *Iphis astronomicus* Koch, 1839; *Laelaspisella epyginalis* Marais and Loots, 1969; *Lucanaspis brachypedes* Costa, 1977; *Myrmeciphis crawleianus* Hull, 1923; *Promacrolaelaps hunteri* Costa, 1971; *Reticulolaelaps faini* Costa, 1968; and *Zontia meliponensis* Turk, 1948. For all these, it was necessary to resort literature-based data.

In some taxa a complete account of morphological characters could not be made because the specimens available were poorly mounted and I had no permission to remount them, or broken and body parts were missing. Example of this are the following taxa: *Angosomaspis*, *Cyclothorax*, *Euandrolaelaps*, *Laelaspisella*, *Myrmeciphis*, *Myrmolaelaps*, *Myrmoleichus*, *Promacrolaelaps*, *Reticulolaelaps*, and *Zontia*.

A total of 50 genera of free-living and arthropod associated laelapids was examined; when necessary and permission was granted, some preparations were remounted.

Methods:

Specimens were studied with the aid of a Wild M-20 phasecontrast microscope, equipped with camera lucida, 15x wide field oculars and 10x, 20x, 40x bright field, 40x phase contrast, 100x bright field and phase contrast objectives. Measurements were made with a 1 mm scale (divisions of 0.01 mm) using the Wild M-20. Dissecting and mounting were accomplished with an Olympus stereoscopic microscope equipped with 10x oculars and 0.7x - 4x objectives.

The morphological terms used are largely those of Evans and Till (1965) for morphological structures, Lindquist and Evans (1965) for idiosomal chaetotaxy, Evans (1963, 1969) for leg chaetotaxy. Moraza and Johnston (in preparation) for tarsus I chaetotaxy and Athias-Henriot (1969) for adenotaxy.

Analytical methods:

One attempt to recover the phylogenetic relationships among the different taxa under study is the Phylogenetic Systematic approach (Felsenstein, 1982; Platnick, 1985). The major criterion and most reliable method for determination of polarities needed in phylogenetic analysis, is the Outgroup method (Watrous and Wheeler, 1981; Farris, 1982; Maddison *et al.*, 1984).

The material utilized for outgroup comparisons was extracted from the families Leptolae-

lapidae Karg, 1978 and Rhodacaridae Oudemans, 1902 (sensu Lee, 1970).

All the data obtained from the study were analyzed using the computational programs PAUP and MacClade. These programs are based in the parsimony principle.

RESULTS AND DISCUSSION

I. HISTORICAL REMARKS

The morphological heterogeneity exhibited by the group has encouraged taxonomic and systematic studies by several scientists who have attempted to define it. Berlese (1892) recognized two families: Dermanyssidae Kolenati, 1859, which included the obligatory parasites, and Laelapidae Berlese, 1892, including the free-living forms, paraphages of arthropods and facultative ectoparasites, comprising the genera *Laelaps* Koch, *Hypoaspis* Canestrini, *Seius* Koch, *Iphis* Koch, *Stylochirus* Canestrini, *Neoberlesia* Berlese, *Podocinum* Berlese and *Iphiopsis* Berlese. In 1903 and 1904 Berlese described new species of free-living and ant associated mites. After Berlese's classification of laelapid mites, the subsequent classificatory works have dealt almost exclusively with the "parasitic" forms. Tragardh (1904, 1908) reduced the family Laelaptidae to subfamily rank and assigned it to the family Parasitidae.

Vitzthum (1943) established one of the current approaches to the classification of this family. Vitzthum recognized a single family, Laelaptidae, with thirteen subfamilies: Hypoaspidinae, Hyletastinae, Phytoseiinae, Podocininae, Iphiopsinae, Haemogamasinae, Laelapinae, Raillietiinae, Liponyssinae, Dermanyssinae, Halarachnidae, Entonyssinae and Rhinonyssinae. With some exceptions, the first five given here included free-living mites or associates of invertebrates and the remaining eight parasites of vertebrates. Baker and Strandtmann (1948), following Vitzthum classification, described *Myrmonyssus chapmani* and included it in the subfamily Hypoaspidinae. Zumpt and Patterson (1951) added a new subfamily, Myonyssoidinae, and tentatively included Dasyponyssinae Fonseca, 1940. However, Zumpt and Till (1958) excluded Myonyssoidinae from Laelapidae and placed it in Ascidae.

A second approach to the interpretation of the Laelapidae was given by Baker and Wharton (1952). They modified Vitzthum's classification and re-

ognized nine families: Laelapidae (Laelapinae, Hypoaspidae and Hyletastinae), Dermanyssidae (Dermanyssinae and Liponyssinae), Phytoseiidae (Phytoseiinae and Podocininae), Iphipsidae, Haemogamasidae, Raillietiidae, Rhinonyssidae, Entonyssidae and Halarachnidae. They mentioned that the Laelapinae have strong ventral setae, expanded pilus dentilis, a fleshy tectum and they are parasitic. On the other hand, Hypoaspidae have weak ventral setae, seta-like pilus dentilis, reduced tectum and they are free-living. The nymphs and adults of Hypoaspidae mites are all active feeding stages, in many cases they may become phoretically associated with other soil-inhabiting arthropods. Hypoaspids have not developed specialized adaptive structures for phoresy, as in other groups of mites, and they cling to their hosts by means of their chelicerae (Hunter and Mollin, 1964) or clasping the host's hair and curving mainly legs II around it (Rosario, 1981). Evans and Till (1966) considered the Hypoaspidae mites one of the most primitive mesostigmatid mites because of the absence of specialized structures. The subfamily Hypoaspidae has been suggested by Radovsky (1969) to have given rise to the parasitic Laelapinae mites from which more specialized parasitic groups (i. e. Dermanyssidae, Spinturnicidae and others) are said to have arisen.

Evans (1955) excluded the Phytoseiinae and Podocininae from Laelapidae. He placed Podocinum near the Macrochelidae and Hypoaspidae in the Laelapinae, and the Raillietiinae in the Liponyssinae. Evans (1957), working with the British free-living and parasitic members of Laelapidae *sensu* Vitzthum, recognized the Eviphididae (=Hyletastinae) as a separate family, but included the Spinturnicinae Oudemans as a subfamily of Laelapidae. Several genera from Laelapinae, Hypoaspidae and Podocininae were removed and distributed among the Aceosejidae and Neoparasitidae. Evans, Sheals and McFarlane (1961) used the name Macronyssinae rather than Liponyssinae. Laelapidae in this narrow sense then included nine subfamilies: Laelapinae, Haemogamasinae, Iphipsinae, Macronyssinae, Entonyssinae, Dermanyssinae, Spinturnicinae, Halarachninae and Rhinonyssinae (Radovsky, 1967).

Bregetova's classification (1956) is similar to that of Baker and Wharton (1952). She gave slightly broader limits for the Laelapidae in which *Raillietia* and *Myonyssus* were included. Tipton (1960) reviewing the Laelapinae recognized in it only fif-

teen genera, all of them vertebrate-associated. He also established the subfamily Alphalaelaptinae with the genus *Alphalaelaps*. Bernhard (1963) mentioned nine subfamilies, but without Spinturnicinae and with Raillietiinae included as a separate subfamily.

In 1965 Karg recognized the superfamily Laelaptoidea Berlese, 1892 *sensu* Evans, 1957 with the single family Laelaptidae. He included subfamilies: Hypoaspidae Vitzthum, 1941 with the genera *Ololaelaps* s. lat. and *Hypoaspis* s. lat., and the subgenera *Cypholaelaps*, *Gymnolaelaps*, *Cosmolaelaps* and *Hypoaspisella*; Laelaptinae Tragardh, 1908 with *Laelaps* and *Haemolaelaps*; Haemogamasidae Oudemans, 1926 with *Eulaelaps* and *Haemogamasus*. Karg (1978a) included the genera *Hypoaspis*, *Androlaelaps* and *Reticulolaelaps* within the family Dermanyssidae Kolenati. Later, in 1979, 1982 and 1987 studying the genus *Hypoaspis* (Dermanyssidae), Karg subdivided the genus into eight subgenera: *Hypohasta* Karg, 1979; *Hypoaspis* Canestrini, s. str., *Cosmolaelaps* Berlese, 1903, *Alloparasitus* Berlese, 1920, *Gaeolaelaps* Tragardh, 1952, *Holostaspis* Kolenati, 1958, *Laelaspis* Berlese, 1903 and *Pneumolaelaps* Berlese, 1920. Till (1963) synonymized *Haemolaelaps* Berlese, 1910 with *Androlaelaps* Berlese, 1903 which was placed by some recent authors in Laelapinae and Hypoaspidae respectively.

Evans and Till (1966, 1979) adopted Dermanyssidae as the family name with priority over Laelapidae. They restricted their concept of the family and recognize the following subfamilies: Dermanyssinae, Haemogamasinae, Pseudolaelapinae, Myonyssinae, Melittiphinae, Laelapinae, Hirstionyssinae and Macronyssinae. They defined a basic dermanyssid type as follows: adult chelicerae chelate-dentate; movable digit bidentate in the female, unidentate in the male; pilus dentilis short, setiform; spermatodactyl free distally and grooved. Deutosternum with six transverse rows of denticles; corniculi horn-like; pedipalps with two-tined claws; anterior margin of tectum denticulate. Dorsal shield entire with 39 pairs of setae. Metasternal setae free. Genital shield flask-shaped with one pair of seta. Anal shield with 3 setae, euanal seta absent. Opisthogastric cuticle with 7 pairs of setae, metapodals small, subcircular. Peritrematal shields free posteriorly; peritreme extending beyond coxa I. Male with holovenal shield bearing 10 pairs of setae excluding anals; genital orifice presternal. All legs with developed

retractile ambulacra; legs' chaetotaxy normal (as defined by Evans and Till, 1965); without marked sexual dimorphism.

Radovsky (1967) delimited the Laelapidae including the Haemogamasinae. He restored Macronyssidae to family rank, and *Hirstionyssus*, *Echinonyssus*, *Patrinyssus*, *Trichosurolaelaps* and *Australaelaps* are placed in the Laelapidae. He restricted Dermanyssidae to members of the Dermanyssinae and elevated Hystriehonyssidae to family rank. Radovsky (1969) chose the restricted family concept Laelapidae in preference to Dermanyssidae s. lat. based on the long established usage of the former name.

Krantz (1978) also retained the name Laelapidae following Radovsky's ideas but he applied the rules of priority in assigning Dermanyssoidea as the superfamily name. He recognized nine subfamilies in Laelapidae: Hypoaspidae which includes many free-living species, many associated with arthropods, and a few regularly found in the nest or on the bodies of vertebrates; Haemogamasinae which are facultative parasites of rodents and some birds, they are polyphagous, feeding on dead arthropods, nematodes or vegetable matter; Laelapinae, facultative parasites of mammals and occasionally with birds; Alphalaelapinae, Myonyssinae and Hirstionyssinae are parasitic on mammals; Iphipsinae and Melittiphinae are associated with arthropods; and Pseudolaelapinae is free-living. Tenorio and Radovsky (1974) also included the subfamily Mesolaelapinae which is found entirely on mammals. In the sense of Krantz (1978) the Laelapidae can be defined as: adults with chelicerae dentate or edentate, fixed digit present; with three pairs of hypostomal setae in nymphs and adults; peritremes variously produced, typically well developed and elongate, occasionally absent; legs without "metatarsi".

Lindquist (1979) gave the Laelapidae the same status as Dermanyssidae. He included under Dermanyssoidea Kolenati, 1859 the families Haemogamasidae, Macronyssidae, Rhinonyssidae, Halacaridae, Spinturnicidae, Ixodorhynchidae, Entonyssidae, Raillietidae, Dermanyssidae and Laelapidae.

Evans and Till (1979) recognized the family Laelapidae with five subfamilies: Laelapinae, free-living mites or with a range of associations with insects, birds and mammals as inhabitants of nests, scavengers and parasites on the body of the host (*Ololaelaps*, *Androlaelaps*, *Ondatraelaps*,

Laelaps, *Hyperlaelaps*, *Pseudoparasitus*, *Stratiolaelaps*, *Cosmolaelaps*, *Holostaspis*, *Gymnolaelaps*, *Pneumolaelaps*, *Laelaspis* and *Hypoaspis* s. lat.); Haemogamasinae, mites associated with house and field mice and moles (*Eulaelaps* and *Haemogamasus*); Myonyssinae, one genus associated with bee-hives (*Myonyssus*); Pseudolaelapinae, a free-living genus (*Pseudolaelaps*); and Hirstionyssinae, an obligatory haematophagous ectoparasite of mammals (*Hirstionyssus*).

Rosario (1981), following Baker and Wharton (1952), recognized the family Laelapidae with two subfamilies: Hypoaspidae and Laelapinae. Among the free-living Hypoaspidae she included: *Cosmolaelaps* Berlese, *Hypoaspis* Canestrini, *Scissuralaelaps* Womersley, *Stratiolaelaps* Berlese, *Gaeolaelaps* Berlese and *Pneumolaelaps* Berlese. For the generic classification, Rosario (1981) followed Tragardh (1952), Costa (1968, 1974) and Hunter (1966), among other authors, who treated these Baker and Wharton (1952) subgenera as valid genera.

Johnston (1982) included the superfamily Dermanyssoidea with seventeen families within the cohort Dermanyssina. He recognized Haemogamasidae and Hirstionyssidae as separate families and not to be included within Laelapidae as Krantz (1978) had done.

From the examples of classifications listed above, it can be clearly seen that there is not precise agreement between any two of these classifications. Furthermore, there are vacillations when it comes to determining the placement of certain taxa. Among these taxa, for example, are: *Urozercon* Berlese, *Myrmonyssus* Berlese, *Podolaelaps* Berlese, *Iphipsis* Berlese, and *Neoberlesia* Berlese. The placement and definition of the genus *Varroa* Oudemans, 1904 has also been controversial. When first described, the genus was considered to have one species *V. jacobsoni*, a parasite of *Apis indica* Fabricius, and was placed into the subfamily Laelapinae. Gunther (1951), based on mites found in the sealed brood cells of honey bees from Singapore, described *Myrmozercon reidii*. Baker and Wharton (1952) listed *Varroa* in the subfamily Hypoaspidae within Laelapidae. Delfinado and Baker (1974) studying mites on honey bees considered *M. reidi* as a synonym of *V. jacobsoni* and proposed the family Varroidae to accommodate two genera: *Varroa* (*V. jacobsoni* Oudemans) and *Euvarroa* (*E. sinhai* Delfinado and Baker); both genera are parasites of domestic and wild honey

bees. Unlike some of the Laelapidae, the females of Varroidae completely lack the fixed digit of the chelicerae and have a reduction in the number of gnathosomal setae. These characters are considered as "unique" for Varroidae by Delfinado and Baker, 1974. In 1987 Delfinado-Baker and Aggarwal described a new species of *Varroa*, *V. underwoodi*, which has also *Apis cerana* (= *A. indica*) as the original host.

II. CLADISTIC ANALYSES

The families Leptolaelapidae and Ologamasidae were used as the sister group and outgroup respectively. Genera like *Leptolaelaps* Berlese, *Ayersacarus* Hunter, *Evansolaelaps* Marais and Loots and *Cerambylaelaps* Costa were originally referred to the family Laelapidae (=Dermanysidae) on account, for example, of the entire dorsal shield, reduced dorsal chaetotaxy, palp-claw 2-tined, 2 pairs of genital setae and male with an entire holovenral shield. However, the long posteriorly directed spermatodactyl is not a shared character with the males of Laelapidae. Karg, 1978b created the subfamily Leptolaelapinae within Macrochelidae to include *Leptolaelaps*. He established that *Leptolaelaps* Berlese, is an "intermediate form" confirming conception of Eviphidoidea Karg, 1965. The superfamily Eviphidoidea is considered the sister group of Dermanyssoidea. Both share the following characters: J4 close to J5, fixed-digit of chelicerae with differentiated dentition and posterior end of dorsum by Z5. Later, in 1983, Karg using phylogenetic methods concluded that Leptolaelapidae is a valid family within Eviphidoidea and the family includes the genera *Leptolaelaps* Berlese, *Ayersacarus* Hunter, *Cerambylaelaps* Costa, *Evansolaelaps* Marais and Loots and *Austrocheles* Karg. These genera are distributed over the southern parts of Africa and South America, over Australia, New Zealand, Malaysia and the subantarctic islands.

Karg, 1983 mentioned that Leptolaelapidae and Laelapidae share the following plesiomorphic characters: slight difference between males and females, dorsal shields with a reticulate pattern, without differences in the shape of dorsal setae, ventral shields not very enlarged and fused, genital shield with one pair of simple setae, anal shield with

two paranal and one postanal setae, deutosternum with 7 to 8 rows of denticles and protonymph pygidial shield with 3 internal, 3 medial and 3 lateral setae.

Among the synapomorphies shared by Laelapidae and Leptolaelapidae are: reduction of the dorsal chaetotaxy, a denticulate tectum, female genital shield flask-shaped, with 1 or 2 pairs of genital setae, metasternal setae off the sternal shield and palp-claw 2-tined.

The used characters, their polarization and data matrix are shown on Tables I and II. Hypotheses about the phylogenetic relationships within the family Laelapidae are shown on Figs. 1 - 9. Numbers on cladograms indicate stems, and the apomorphic characters are listed for each stem.

On the basis of the evidence summarized on the cladograms it appears that the genera of free-living and arthropod-associated laelapid mites represent 8 main, well defined and probably monophyletic groups. These are referred to as groups I, II, III, IV, V, VI, VII and VIII (Fig. 1). Phylogeny within each group is discussed separately followed by a discussion of the relationships among them and with the laelapid associate of vertebrates. In the text character numbers are given in parentheses.

Group I (Fig. 2):

This group includes all the free-living, soil-dwelling, predatory genera: *Ololaelaps*, *Pseudoparasitus*, *Gaeolaelaps*, *Alloparasitus*, *Cosmolaelaps*, *Euandrolaelaps* and *Stratiolaelaps*.

The free-living forms show little diversity in morphology, and the genera of this group are plesiomorphic for nearly all of the characters that have been analyzed. For this reason it can not be defined satisfactorily on the basis of unique derived characters (groups autapomorphies); apomorphies are: one postero-lateral seta (pl2) on genu II absent (53), a state which is also derived independently in *Coleolaelaps* and *Dyscinetonyssus*, and seta antero-dorsal two (ad2) on tibia II absent (65), independently derived in *Hypoaspis* and *Coleolaelaps*.

The species of *Ololaelaps* are symplesiomorphic for most of the characters considered here and probably resemble the ancestral laelapid stock in many ways. A peritrematal shield fused to the exopodal shields (36) in the female is the only apomorphy for *Ololaelaps*, a character state which has also evolved independently in *Cosmolaelaps* and *Coleolaelaps*.

The group of genera formed by *Pseudoparasitus*, *Cosmolaelaps*, *Gaeolaelaps*, *Stratiolaelaps*, *Euandrolaelaps* and *Alloparasitus* apomorphically developed additional setae (px) between the J and Z series (31). *Pseudoparasitus* is an early derived taxon with opisthonotal seta S5 absent (32), which evolved independently at least three times within the laelapids. The *Cosmolaelaps*-*Alloparasitus* group of genera present a two-tined palp claw (15); character state which is the predominant one in most of the laelapids with the exception of *Ololaelaps*, *Pseudoparasitus* and *Gymnolaelaps* which retain the primitive condition of three-tined palp claw.

Cosmolaelaps presents characters 30 and 36 as apomorphies. *Stratiolaelaps* has evolved four apomorphies: long corniculi, longer than palp femur (13); podonotal seta z2 absent (20); opisthonotal seta S5 not on the shield (32) and one antero-ventral seta (av2) on genu I absent (49). *Euandrolaelaps* evolved a short peritreme (34), and in *Alloparasitus* the podonotal seta z2 is absent (20). *Gaeolaelaps* is not defined by any apomorphic or autapomorphic characters among the ones analyzed. This problem might be partly resolved by restricting *Gaeolaelaps* to the "aculeifer group".

Group II (Fig. 3):

This group includes *Androlaelaps casalis*, a predator, and the paraphages of Coleoptera (*Hypoaspis*, *Coleolaelaps* and *Dyscinetonyssus*) and Blattaria (*Blaberolaelaps* and *Gromphadorholaelaps*). This group of laelapid genera emerged from its sister group, the free-living laelapids, by one autapomorphic character: absence of podonotal seta r6 on the dorsal shield (23).

Androlaelaps casalis has three apomorphies: podonotal seta s6 not on the shield (22), unpaired accessory setae between J series present (30) and additional setae (px) between J and Z series present (31). It is the sister group of the *Hypoaspis* through *Gromphadorholaelaps* group of genera which are characterized by the loss of the podonotal seta z3(21).

Hypoaspis and *Coleolaelaps* share one character: the absence of one antero-dorsal seta (ad2) on tibia II (65). *Coleolaelaps* is differentiated from its sister genus by characters 28, 32 and 53; *Hypoaspis* cannot be defined with any of the characters used here.

From the *Hypoaspis*-*Coleolaelaps* group diverged a group of genera formed by *Dyscinetonyssus*, *Blaberolaelaps* and *Gromphadorholaelaps*, which share three apomorphies: reduced hypostomal process (11), less than two teeth on the movable digit of the female chelicera (18) and a short peritreme, reaching to coxa II-III (34). *Dyscinetonyssus* and *Blaberolaelaps* present two synapomorphies: loss of the opisthonotal setae J2 (24) and Z3 (29), and three apomorphic characters, 20, 22 and 32, which also evolved independently in some predatory laelapids (i.e., *Alloparasitus*, *Coleolaelaps* and *A. casalis*). *Gromphadorholaelaps* presents one to three denticles per row on the deutosternum (9), and one autapomorphy: fixed digit of male chelicerae with same length as the spermatodactyl (78).

Dyscinetonyssus differentiated from its sister genus by developing fourteen apomorphies: more than 6-7 rows of deutosternal denticles (8), a character state which also is derived independently in *Neohypoaspis* and some laelapid associates of mammals (*Haemogamasus*, *Myonyssus* and *Echinyonyssus*); a reduced fixed digit on the female chelicera (17), a state also present in *Myrmolaelaps*, *Varroa*, *Androlaelaps fahrenheiti* and *Alpha-laelaps*; podonotal seta z4 spine-like (19); loss of the opisthonotal seta Z2 (28); genital seta off the shield (43); loss of setae ad3 (47) and av2 (49) on genu I; setae ad3 (52) and pl2 (53) on genu II absent; seta pd3 on genu IV absent (56); loss of setae ad3 (60), pd3 (61), av2 (62) and pl2 (63) on tibia I. On the other hand, *Blaberolaelaps* is differentiated by losing the opisthonotal seta Z1 (27), and by one unique derived character: trochanter of female palp with one hyaline and flat seta (80).

Group III (Fig. 4):

This group includes seven genera associated with Hymenoptera (Formicidae and Apidae): *Gymnolaelaps*, *Holostaspis*, *Laelaspis*, *Myrmonyssus*, *Pneumolaelaps*, *Hunteria*, and *Laelaspoides*, which share one apomorphic character: loss of seta (ad2) on tibia II (65).

The *Pneumolaelaps*-*Holostaspis* group is defined by one synapomorphic character: sternal seta st4 placed on the endopodals (42). *Pneumolaelaps* is an early derived taxon with two autapomorphies: sternal seta st1 placed off sternal shield, on the metasternal area (37) and a wide peritreme (82). Its

TABLE I. List of Characters.

1-4. Tectum:		20. Podonotal seta z2:		37. Sternal seta st1	
1. trifurcate	1000	present	0	placed on sternal shield	0
2. denticulate	1100	absent	1	placed off sternal shield	1
3. smooth	1110				
4. fimbriate	1101	21. Podonotal seta z3:		38-42. Sternal seta st4:	
example:		present	0	38. on sternal shield	00000
<i>Pseudolaelaps</i>	1000	absent	1	39. on metasternal shield	10000
<i>Gaeolaelaps</i>	1100			40. on soft cuticle	11100
<i>Laelaps</i>	1110	22. Podonotal seta s6:		41. on endopodal	11101
<i>Haemogamasus</i>	1101	present	0	42. absent	11110
		absent	1		
5. Subcapitular setae hyp 3:		23. Podonotal seta r6:		43. Genital seta:	
present	0	present	0	on the shield	0
absent	1	absent	1	off the shield	1
6-8. Number of rows of		24. Opisthonotal seta J2:		44. Female anal shield:	
deutosternal denticles:		present	0	fused with ventral and	
6. 6-7 rows	000	absent	1	genital shield	0
7. less than 6 rows	110			free	1
8. more than 7 rows	101	25. Opisthonotal seta J3:		45. Shape female anal shield:	
example:		present	0	subtriangular, subcircular	
<i>Gaeolaelaps</i>	000	absent	1	or suboval	0
<i>Varroa</i>	110			other shape (kidney, crescent,	
<i>Haemogamasus</i>	101	26. Opisthonotal seta J4:		bowl shaped)	1
		present	0		
9. Number of deutosternal denticles:		absent	1	46. Seta al2 GeI:	
multidenticulate	0	27. Opisthonotal seta Z1:		present	0
1-3 denticles	1	present	0	absent	1
		absent	1	47. Seta ad3 Ge I:	
10. Tritosternum:				present	0
long, bifid	0	28. Opisthonotal seta Z2:		absent	1
short, lacinia reduced	1	present	0		
		absent	1	48. Seta pd3 Ge I:	
11. Hypostomal processes:				present	0
normal, fimbriate	0	29. Opisthonotal seta Z3:		absent	1
reduced	1	present	0		
		absent	1	49. Seta av2 Ge I:	
12-14. Length of corniculi:				present	0
12. not longer than palp femur	000	30. Unpaired accessory setae		absent	1
13. longer than palp femur	110	between J series:			
14. one-half palp femur	101	absent	0	50. Seta pl2 Ge I:	
		present	1	present	0
15. Palpal claw:				absent	1
with 3 tines	0	31. Additional setae (px's):			
with 2 tines	1	always absent	0	51. Seta al2 Ge II:	
		present	1	present	0
16. Size of palp claw tines:				absent	1
similar in length	0	32. Opisthonotal seta S5 on the			
basal tine reduced	1	shield:		52. Seta ad3 Ge II:	
		present	0	present	0
17. Fixed digit female chelicera:		absent	1	absent	1
normally developed	0				
reduced or absent	1	33-35. Length peritreme:		53. Seta pl2 Ge II:	
		33. long (i.e., reaching coxa I)	000	present	0
18. Number of teeth on movable		34. short (i.e., reaching		absent	1
digit female chelicera:		coxae III-II)	110		
two teeth	0	35. absent	111	54. Seta al2 Ge III:	
one or none	1			present	0
				absent	1
19. Podonotal seta z4:		36. Female peritrematal shield:			
normal, setiform	0	not fused to exopodal IV	0		
spine-like or blunt-like	1	fused to exopodal IV	1		

55. Seta al2 Ge IV: present absent	0 1	65. Seta ad2 Ti II: present absent	0 1	75. Length of legs I: subequal in length twice longer than other legs	0 1
56. Seta pd3 Ge IV: present absent	0 1	66. Seta pl2 Ti II: present absent	0 1	76. Femur IV: without anterior spur with anterior spur	0 1
57. Seta pv1 Ge IV: present absent	0 1	67. Seta al2 Ti III: present absent	0 1	77. Fixed digit female chelicera: without anterior process with anterior process	0 1
58. Seta pl2 Ge IV: present absent	0 1	68. Seta ad2 Ti III: present absent	0 1	78. Fixed digit male chelicera: shorter than the spermadactyl same length as the spermadactyl	0 1
59. Seta al2 Ti I: present absent	0 1	69. Seta pl2 Ti III: present absent	0 1	79. Sternal setae on Protonymph: normal hypertrophied	0 1
60. Seta ad3 Ti I: present absent	0 1	70. Seta al2 Ti IV: present absent	0 1	80. Palpal-trochanter setae: all simple one hyaline and flat seta	0 1
61. Seta pd3 Ti I: present absent	0 1	71. Seta ad2 Ti IV: present absent	0 1	81. Male dorsal shield: entire divided	0 1
62. Seta av2 Ti I: present absent	0 1	72. Seta pd3 Ti IV: present absent	0 1	82. Wide peritreme: absent present	0 1
63. Seta pl2 Ti I: present absent	0 1	73. Sternal shield: well sclerotized not sclerotized	0 1	83. Podonotal seta j1: simple spatulated	0 1
64. Seta al2 Ti II: present absent	0 1	74. Number of setae on anal shield: 2 o three more than three	0 1		

TABLE II. Data Matrix.

Character Number	12345 12345	67890 67890	12345 12345	67890 67890	12345 12345	67890 67890	12345 12	67890
<i>Pseudoparasitus</i>	11000 00010	00000 00000	00000 00100	00000 01100	00000 00001	00000 00110	11000 10	00111
<i>Cosmolaelaps</i>	11000 00010	00000 00000	00001 00100	00000 01100	00000 00001	00001 00110	10000 10	10111
<i>Euandrolaelaps</i>	11000 00010	00000 00000	00001 00100	00000 01000	00000 00001	00000 00110	10110 10	00111
<i>Gaeolaelaps</i>	11000 00010	00000 00000	00001 00100	00000 01100	00000 00001	00000 00110	10000 10	00111
<i>Ololaelaps</i>	11000 00000	00000 00000	00000 00100	00000 01100	00000 00001	00000 00110	00000 10	10000
<i>Alloparasitus</i>	11000 00010	00000 00000	00001 00100	00001 01100	00000 00001	00000 00110	10000 10	00111
<i>Stratiolaelaps</i>	11000 00010	00000 00010	01101 00100	00001 01100	00000 00001	00000 00110	11000 10	00111
<i>Coleolaelaps</i>	11000 00010	00000 00000	00001 00100	00000 01100	10100 00001	00100 00100	01000 10	10111
<i>Dyscinetonyssus</i>	11000 00110	10100 01010	10001 01100	01111 11101	01110 11101	00110 10110	01110 11	00111
<i>Hypoaspis</i>	11000 00010	00000 00000	00001 00000	00000 01100	10000 00001	00000 00110	00000 10	00111
<i>Gymnolaelaps</i>	11000 01010	11000 00000	00000 00000	00001 00100	00000 00001	00001 00100	11000 10	00111
<i>Holostaspis</i>	11100 01010	00001 00000	00001 00000	00100 00100	00000 00001	00001 00110	10000 10	00111
<i>Laelaspis</i>	11100 01000	00000 00000	00001 00010	00001 01100	00000 00001	00001 00110	00000 10	00111
<i>Myrmolaelaps</i>	11100 00010	00001 00010	10001 00000	11100 00100	01100 00001	00001 00100	10110 10	10000
<i>Myrmonyssus</i>	11101 10110	00000 11101	10001 11111	10100 10111	11100 11111	10000 11111	01110 11	00111
<i>Neoberlesia</i>	11101 00001	00000 00000	10001 00000	00100 00100	00100 00001	00001 00110	10000 10	00000
<i>Bisternalis</i>	11100 01011	00000 10110	00001 00000	00000 00100	01100 10000	00001 00010	11000 00	01111
<i>Euvarroa</i>	11101 00011	11001 00100	10001 01000	11000 10100	00000 00000	00001 00000	10110 00	00111
<i>Hunteria</i>	11100 00010	11000 00000	00001 01000	00000 00000	00000 00001	00001 00100	11110 10	00111
<i>Laelaspoides</i>	11101 01010	00000 00000	00001 00000	00001 10100	01100 00001	00001 00110	10000 10	00111
<i>Melittiphis</i>	11100 00011	11010 00000	10001 00100	00000 01100	00000 00101	00001 10110	10000 10	00000

<i>Melittiphisoides</i>	11100 00010	11000 00100	10001 00000	00000 11100	01100 10001	00001 00110	11110 10	01000
<i>Neohypoaspis</i>	11000 00011	10100 00000	10001 00000	00000 00100	01100 00001	00001 00110	10000 10	10000
<i>Pneumolaelaps</i>	11100 01010	00000 00000	00001 00000	00000 00100	00000 00001	00000 00110	00000 10	01111
<i>Stelvus</i>	11101 00010	00001 01010	00001 01000	00111 01100	00100 01000	10000 00110	01110 10	01111
<i>Tropilaelaps</i>	11101 00011	00010 00000	11011 01100	10000 00000	00000 00000	00001 00110	10000 00	00111
<i>Varroa</i>	11101 00010	11011 00010	10001 00000	11100 01100	00000 01000	00001 00110	10110 10	00000
<i>Dinogamasus</i>	11100 00111	00000 00000	10001 00000	10000 00000	00000 00000	00001 00100	10110 10	00111
<i>Blaberolaelaps</i>	11100 00010	00010 00000	10001 00000	10100 00100	10100 00000	00000 00010	00110 10	00111
<i>Urozercon</i>	11101 10011	00000 01111	11011 01000	00100 10101	00000 11101	00001 10110	10000 11	00111
<i>Iphiopsis</i>	11101 00011	00000 11111	11101 11111	00000 11111	01100 10111	00010 11111	01110 11	00111
<i>Jacobsonia</i>	11001 00010	00000 11111	11101 11111	00000 11111	11111 11111	00010 11111	01111 11	01111
<i>Narceolaelaps</i>	11001 00010	00010 11111	10001 01000	00000 10011	01100 11101	01000 10010	01110 11	00111
<i>Julolaelaps</i>	11001 00010	00000 00000	10001 00000	00000 00100	01100 00000	00010 00100	11110 10	00111
<i>Scissuralaelaps</i>	11100 00010	00000 00110	01101 00000	00000 00000	00000 11000	00000 00110	10000 10	00111
<i>Iphiolaelaps</i>	11101 00010	11000 11111	10001 11111	00100 10111	01100 11110	00000 11111	11111 01	00111
<i>Scolopendracarus</i>	11101 00010	11011 11011	10001 01110	00000 11101	00110 01000	10100 00110	01110 11	01111
<i>Ljunghia</i>	11000 00010	11000 00000	10001 00000	00100 00100	11101 01000	00100 00110	01000 10	00111
<i>Cyclothorax</i>	11000 00010	11000 11111	11011 00000	00100 01111	01101 11100	10000 10110	11000 10	01111
<i>Gecarcinolaelaps</i>	11100 10010	11001 01100	10001 01000	00000 01001	00000 10001	00001 00101	10000 10	00111
<i>Haemogamasus</i>	11010 00010	10100 00000	10001 00000	00100 01000	00000 00000	00001 00110	10110 01	10111
<i>Androcasalis</i>	11100 00010	00000 00000	00001 00000	00100 01000	01100 00000	00001 00110	10000 10	00111
<i>Androfahrenheitzi</i>	11100 00010	00000 00000	00001 00000	01000 01100	00000 00000	10011 00110	10000 10	00111
<i>Myonyssus</i>	11100 00011	10110 00000	10001 00000	00101 01100	01000 00000	00000 00110	11110 10	00111

[illegible]

Note: Characters 73 to 83 are not included here due to the fact that each of them is an autopomorphy of a different genus.

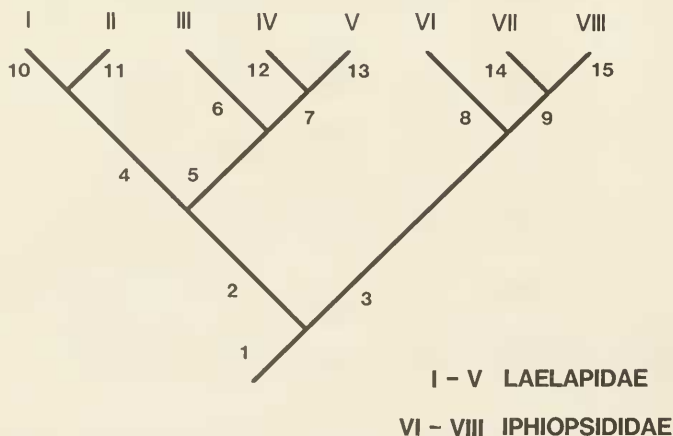


FIG. 1. Families Laelapidae and Iphiopsididae. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 1, 2, 38, 39, 40, 44, 58, 68, 69, 71; STEM 2: 58; STEM 3: 62; STEM 4: 57; STEM 5: 3; STEM 6: 65; STEM 7: 30, 45; STEM 8: 3, 12, 13, 48, 49, 61; STEM 9: 11, 22, 23, 32, 58; STEM 10: 53, 65; STEM 11: 23; STEM 12: 22, 23; STEM 13: 5; STEM 14: 5, 34; STEM 15: 7.

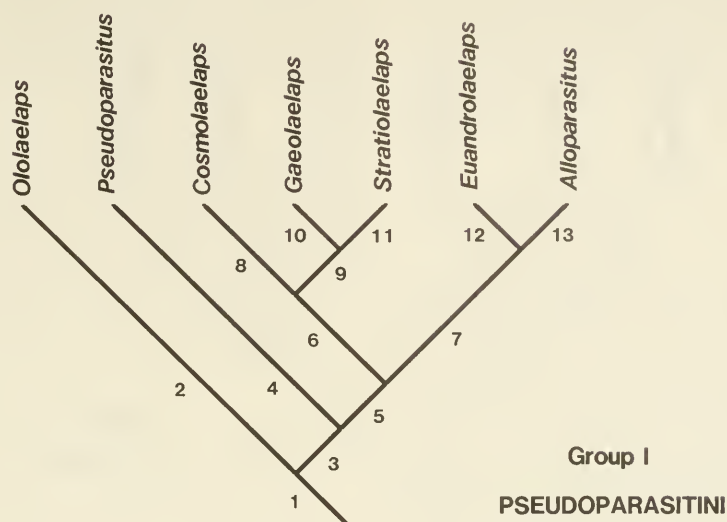


FIG. 2. Group I: Pseudoparasitini. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 53, 65; STEM 2: 36; STEM 3: 31; STEM 4: 32; STEM 5: 15; STEM 6: —; STEM 7: —; STEM 8: 30, 36; STEM 9: —; STEM 10: —; STEM 11: 12, 13, 20, 32, 49; STEM 12: 3, 4; STEM 13: 20.

sister group is characterized by having unpaired accessory setae between the J series (30). *Holostaspis* is differentiated by a short, reduced tritosternum (10), and reduced number of teeth (one or none) on the movable digit of the female chelicera (18).

Laelaspoides and *Laelaspis* are closely related genera which present one synapomorphic character podonotal seta z2 absent (20), state which also evolved independently in some free-living laelapids. *Laelaspis* differentiated from its sister group by two progressive apomorphies: loss of seta al2 on genu III (54) and pvl on genu IV (57). On the other hand, *Laelaspoides* developed three apomorphic characters: loss of podonotal seta s6 (22) and r6 (23) on the dorsal shield, and loss of seta pd3 on genu IV (56), a parallelism with *Myrmonyssus*.

The sister group of *Pneumolaelaps-Holostaspis* is *Hunteria-Myrmonyssus*, which includes species that have three apomorphic characters: opisthonotal seta S5 not on the shield (32), a short peritreme (34) and seta antero-dorsal three (ad3) on genu II is absent (52). The early derived taxon is *Myrmonyssus* with 28 apomorphies: characters 5, 11, 16, 18, 21,

26, 32, 34, 46-48, 50-56, 59-64, 66, 67, 70 and 72. *Hunteria* evolved less than 6-7 rows of deutosternal denticles (7), opisthonotal seta S5 not on the shield (32) and seta ad3 on genu II absent (52). *Gymnolaelaps* presents one apomorphic characters-podonotal seta z2 absent (20).

Hunteria and *Gymnolaelaps* present two synapomorphies: less than 6-7 rows of deutosternal denticles (7) and unpaired accessory setae between the J series present (30).

Group IV (Fig. 5):

The *Bisternalis - Melittiphisoides* group of genera which evolved two synapomorphies: podonotal setae s6 (22) and r6 (23) absent.

The distribution of character states summarized in Fig. 5 suggests an early division of this group into four principal lineages. The first lineage represents *Bisternalis*, taxon defined by three autapomorphic characters at this level: sternal seta st4 on the endopodal shield (42), seta al2 on genu I

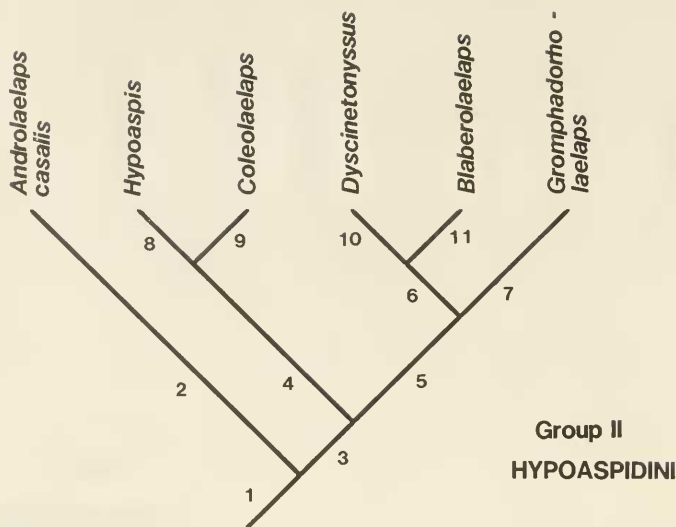


Fig. 3. Group II: Hypoaspidini. Numbers on the figure refer to stems. Apomorphic characters are listed for each stems. STEM 1: 23; STEM 2: 22, 30, 31; STEM 3: 21; STEM 4: 65; STEM 5: 11, 18, 34; STEM 6: 20, 22, 23, 24, 29; STEM 7: 9; STEM 8: —; STEM 9: 28, 32, 53; STEM 10: 8, 17, 19, 28, 43, 47, 49, 52, 53, 56, 60, 61, 62, 63; STEM 11: 27.

absent (46), seta av2 on genu I absent (49) and seta pd3 on tibia I absent (61), and a convergent development of three apomorphies: opisthotal seta S5 not on the shield (32), sternal seta st4 placed off the shield (37) and seta pd3 on genu I absent (48).

A second lineage represents an unnamed taxon defined by two synapomorphies: hypostomal process reduced (11) and the loss of seta ad2 on tibia II (65). The early derived taxa from this lineage are *Myrmolaelaps* and *Neoberlesia* which can be tentatively defined by one progressive synapomorphy: a reduced number of teeth (less than two) on movable digit of female chelicera (18). *Myrmolaelaps* further became differentiated with four apomorphies (10, 16, 34, 37) and one autapomorphic character: a reduced fixed digit of female chelicera (17), and legs I twice longer than other legs (75), while *Neoberlesia* achieved two apomorphies: seta hyp 3 of the gnathosoma absent (5), and femur IV with an anterior spur (76).

The third lineage represents *Neohypoaspis* which can be defined by two apomorphies: more than 6-7 rows of deutosternal denticles (8) and female peritrematal shield fused to exopodal IV shield (36) a state also derived independently in

Myrmolaelaps. *Neohypoaspis* presents spatulated podonotal setae j1 (83).

A fourth lineage represents two nominate genera, *Melittiphis* and *Melittiphisoides*, with two synapomorphies: less than 6-7 rows of deutosternal denticles (7) and seta pv1 on genu IV absent (57). *Melittiphis*, originally placed in the subfamily Melittiphinae by Evans and Till (1966) presents four autapomorphic characters: one denticle per deutosternal row (9), loss of setae pl2 on genu II (53), pl2 on tibia I (63) and pl2 on tibia II (66); and *Melittiphisoides* evolved seven apomorphies (32, 33, 34, 37, 48, 56 and 61).

Group V (Fig. 6):

The genera in this group lack the hypostomal setae three (hyp3) or one (hyp1) on the subcapitulum (5). The early derived taxa are the *Tropilaelaps-Urozercon* group, which are closely related genera, sharing three synapomorphies: a reduced hypostomal process (11), a state which also evolved independently once in the *Euvarroa-Dinogamasus* group; reduced corniculi (i.e., reaching to half palp-

femur length) (14) and loss of seta ad3 on genu II (52). *Urozercon* has five apomorphies: 18, 47, 48 and 62, and four autapomorphic characters: sternal seta four (st4) absent (42), loss of setae pd3 (61) and pl2 (63) on tibia I, and five setae on the anal shield (74).

Its sister group *Stevelus*, *Euvarroa*, *Varroa* and *Dinogamasus* is defined by a regressive synapomorphy: short peritreme (34). The first taxon to differentiate in this lineage is *Stevelus*, with characters 10, 18, 32, 49, 52 and 57 as apomorphies and five autapomorphies: seta z4 blunt-like (19), loss of podonotal seta z2 (20), loss of opisthonotal seta J4 (26), sternal seta one (st1) placed off the shield (37) and loss of seta ad3 on genu I (47).

The lineage which originated the remaining genera on group V present one synapomorphic character, which is an autapomorphy for the group: palp-claw with basal tine reduced (16); and apomorphic character (11), a parallelism with the *Tropilaelaps-Urozercon* group. *Dinogamasus* has evolved one apomorphy: sternal seta four (st4) placed on soft cuticle (43), a state which also has evolved independently in some of the free-living forms. From this lineage emerged the *Euvarroa-Varroa* group with two autapomorphies: tritos-ternum short and reduced (10) and fixed digit of female chelicera absent (17). *Varroa* and *Euvarroa* have been originally included in a separate family - Varroidae - by Delfinado and Baker (1974) - on the basis of the complete lack of the fixed digit, and the number and arrangement of the gnathosomal setae. However, these regressive apomorphies have evolved independently in several other genera in the family Laelapidae. These authors missed the fact that *Tropilaelaps* and *Stevelus* lack seta hyp3, *Dinogamasus* and *Urozercon* lack setae hyp1 on the gnathosoma, and that *Myrmolaelaps* also presents a very reduced (sometimes regarded as a total absence) fixed digit on the female chelicera.

Varroa is differentiated from its sister genus, *Euvarroa*, by regressive autapomorphies: loss of setae av2 on genu I (49), pv1 on genu IV (57) and av2 on tibia I (62). *Euvarroa* presents two autapomorphies: loss of setae pd3 on genu I (48) and ad3 on genu II (52).

Group VI (Fig. 7):

This lineage represents one genus, *Scissura-laelaps*, which is differentiated by two apomor-

phies: smooth tectum (3); corniculi longer than palp femur (12-13), a parallelism with *Stratiolaelaps*; and two regressive characters: loss of setae pd3 (48) and av2 (49) on genu I. This is the sister group of the remaining genera associated with Diplopoda and Chilopoda.

Group VII (Fig. 8):

This lineage represents a group of genera formed by *Julolaelaps*, *Iphiolaelaps*, *Iphiopsis*, *Jacobsonia*, *Narceolaelaps* and *Scolopendracarus*. It is defined by one regressive synapomorphy: hypostomal seta three (hyp3) absent (5).

Julolaelaps is the first taxon to differentiate with only one apomorphy: loss of the opisthonotal seta Z3 (29). Its sister lineage in turn is defined by characters 49, 50 60 and 61 as apomorphies, and by five synapomorphies, which are autapomorphic within the group: loss of setae al2 (46) and ad3 (47) on genu I, loss of setae ad3 on genu II (52), pd3 on genu IV (56) and pd3 on tibia IV (72). *Scolopendracarus* has separated from its sister group of genera by nine apomorphic characters (9, 10, 24, 25, 26, 28, 53, 54 and 57), and by one autapomorphic character: sternal shield not sclerotized (73).

The group *Iphiolaelaps-Narceolaelaps* has evolved one autapomorphy: loss of seta al2 on tibia I (59) and three regressive apomorphies: loss of setae pd3 on genu I (48), pl2 on tibia I (63) and pl2 on tibia I (66).

Narceolaelaps is the first taxon to emerge from this lineage by evolving one autapomorphic character: loss of the opisthonotal seta Z1 (27) and two apomorphies: one to three denticles per deutosternal row (9), a state which also evolved independently in *Scolopendracarus*, and loss of seta ad2 on tibia II (65), a parallelism with the *Iphiopsis - Jacobsonia* group. Males of *Narceolaelaps* present a divided dorsal shield (81).

The *Iphiolaelaps-Jacobsonia* group has evolved seven synapomorphic characters (51, 53, 54, 55, 64, 67 and 70); from which four are apomorphies within the group: loss of setae al2 on genu II (51), al2 on genu IV (55), al2 on tibia II (64) and al2 on tibia III (67). *Iphiolaelaps* is an early derived taxon with two apomorphic characters: one tooth on the movable digit of the female chelicera (18), a state which also has evolved independently in *Ljunghia* and *Cyclothorax*, and lack of a peritreme (35), which is a parallelism with *Jacobsonia*.

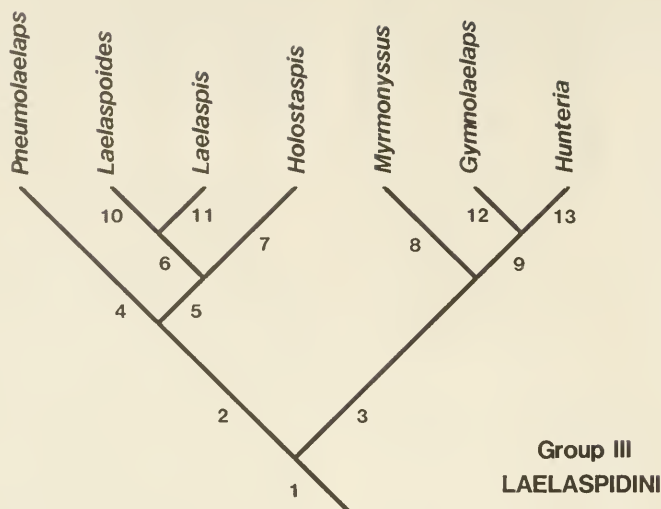


Fig. 4. Group III: Laelaspidini new tribe. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 65; STEM 2: 42; STEM 3: 32; STEM 4: 37; STEM 5: 30; STEM 6: 20; STEM 7: 10, 18; STEM 8: 5, 11, 16, 18, 21, 22, 23, 26, 34, 43, 46, 47, 48, 50, 51, 52, 53, 54, 55, 56, 59, 60, 61, 62, 63, 64, 66, 67, 70, 72; STEM 9: 6, 7, 30; STEM 10: 5, 22, 23, 56; STEM 11: 54, 57; STEM 12: 20; STEM 13: 33, 34, 52.

Jacobsonia and *Iphiopsis* present five synapomorphies: corniculi longer than palp-femur (13), opisthonotal seta Z3 absent (29), loss of seta pv1 on genu IV (57) and ad2 on tibia II (65). *Jacobsonia* is differentiated by three apomorphic characters: loss of podonotal seta z3 (21) and opisthonotal seta J2 (24), lack of a peritreme (35), sternal seta one (st1) placed off the shield (37), and one autapomorphic character: fixed digit of females chelicerae with a process directed anteriorly (77).

Group VIII (Fig. 9):

Lineage that represents taxon which includes the genera *Ljunghia*, *Gecarcinolaelaps* and *Cyclothorax*. It is defined by only one apomorphy: less than 6-7 rows of deutosternal denticles (6-7). It seems that *Ljunghia* is not a well defined taxon (Domrow, 1975) because all the species included are very different from each other. *Ljunghia*, in the present sense, could be defined by characters 18, 21, 25 and 28, which represent parallelisms with other genera of Laelapidae.

Its sister group, *Gecarcinolaelaps* -*Cyclothorax*, evolved four progressive apomorphies: loss of seta pd3 on genu I (48), pv1 on genu IV (57), ad3 on tibia I (60) and seta pd3 on tibia I (61). *Cyclothorax* is differentiated by ten apomorphies (12, 14, 18, 25, 26, 37, 49, 50, 63, 66), and *Gecarcinolaelaps* by a short and reduced tritosternum (10), unpaired accessory setae between the J series present (30), sternal seta st4 absent (41), loss of setae ad3 on genu II (52) and al2 on tibia IV (70); and by one autapomorphy: sternal setae of the protonymph hypertrophied (79).

Relationships among groups I-VIII (Fig. 1):

While each of the groups (I - VIII) are reasonably well defined on the basis of synapomorphies and probably monophyletic, the family Laelapidae appears to be weakly characterized.

The Cladogram on Fig. 1 is supported by seven synapomorphies, shared by almost all the members included in this group of genera, and considered results of regressive evolution: a) loss of

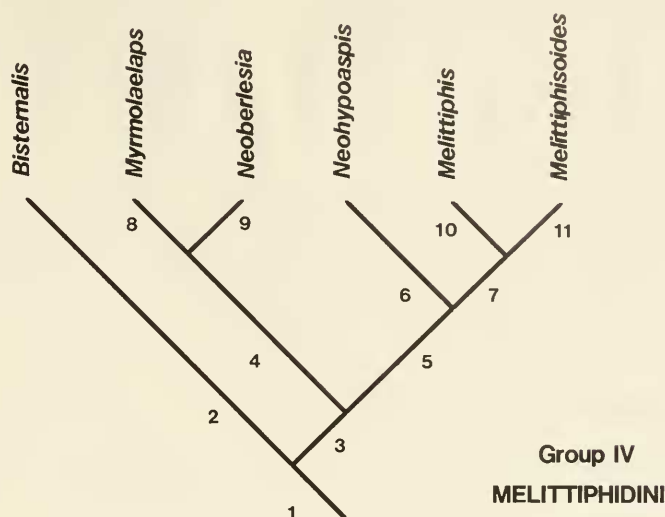


FIG. 5. Group IV: Melittiphidini. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 22, 23; STEM 2: 32, 37, 42, 46, 48, 49, 61; STEM 3: 11, 65; STEM 4: 18; STEM 5: —; STEM 6: 8, 36; STEM 7: 7, 57; STEM 8: 16, 17, 33, 34, 36, 49; STEM 9: 5; STEM 10: 9, 53, 63, 66; STEM 11: 32, 33, 34, 37, 48, 56, 61.

seta postero-lateral two (pl2) on genu IV, with the exception of *Hunteria*, *Tropilaelaps*, *Dinogamasus*, *Gromphadorholaelaps*, *Narceolaelaps*, *Scissuralaelaps* and *Gecarcinolaelaps*; b) loss of seta ad2 on tibia III, except in *Bisternalis*, *Euvarroa*, *Blaberolaelaps*, *Narceolaelaps*; c) loss of seta pl2 on tibia III, except in *Dinogamasus*, *Narceolaelaps*, *Coleolaelaps*, *Myrmolaelaps*, *Euvarroa* and *Hunteria*; d) loss of seta ad2 on tibia IV, with the exception of *Tropilaelaps*, *Gromphadorholaelaps*, *Iphiolaelaps*, *Bisternalis* and *Euvarroa*; e) tectum not trispinate (denticulate or smooth); f) sternal seta four (st4) placed off the sternal shield, with the exception of *Ololaelaps*, *Myrmolaelaps*, *Melittiphisoides*, and *Neohypoaspis*, and g) female anal shield free and triangular except on *Ololaelaps* and *Neoberlesia*.

Grandjean (1946) gave several examples on priorities in setal regression and it seems clear that losses usually occur in identical sequences even in different lineages of the same major group. When dealing with presence or absence of body or leg setae as parallelism or convergence, it is common to find high homoplasy. It is my contention that the cladogram on Fig. 1 is the least easily rejected

despite the relatively large amount of homoplasy, as shown by the relatively great tree length and the low consistency index.

The results of the analyses indicate that the Hypoaspidae (Groups I to II) is the sister group of the other Laelapidae (Groups III - V).

Groups I and II are supported by one synapomorphic character, which is a regressive autapomorphy: loss of seta pv1 on genu IV (57). Groups I - II share only one synapomorphy with groups III - V, which is also a regressive autapomorphy, the loss of seta pl2 on genu IV (58).

Groups III - V present one synapomorphic character: smooth tectum (3), with *Gymnolaelaps* and *Neohypoaspis* as exceptions. *Gymnolaelaps* has been defined by Evans and Till (1966) as a group of species with a denticulate tectum, and *Neohypoaspis* also presents a denticulate tectum. Group III is defined by a regressive apomorphy: loss of seta ad2 on tibia II, state which also evolved independently on group I (freeliving laelapids).

Groups IV and V share two synapomorphies: unpaired accessory setae between J series present (30), with the exception of *Stelvelus* and *Myrmonyssus*; and female anal shield kidney, crescent or

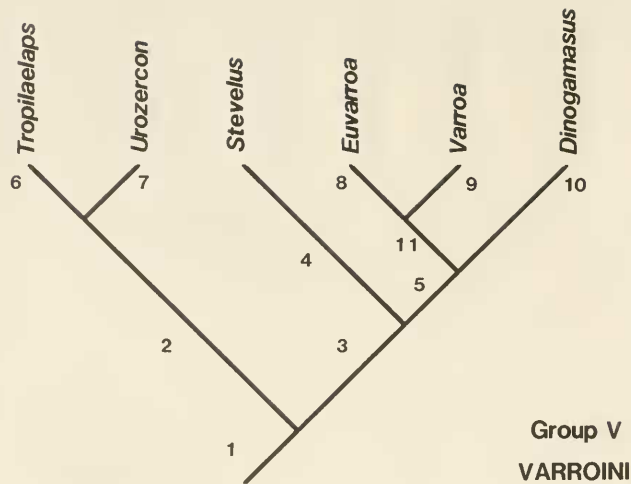


FIG. 6. Group V: Varroini. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 5; STEM 2: 11, 14, 52; STEM 3: 34; STEM 4: 10, 18, 19, 20, 26, 32, 37, 47, 49, 57; STEM 5: 16, 11; STEM 6: 50; STEM 7: 18, 42, 47, 48, 49, 50, 61, 62, 63; STEM 8: 48, 52; STEM 9: 9, 49, 57, 62; STEM 10: 43; STEM 11: 10, 17.

bowl shaped (45): exceptions are *Myrmolaelaps*, *Melittiphisoides*, *Stevelus* and *Varroa*. Group IV is defined by two synapomorphies: podonotal setae s6 (22) and r6 (23) not on the dorsal shield, absent or inserted on the lateral soft cuticle. Group V is characterized by lacking seta hyp 3 on the subcapitulum (5).

On the other hand groups VI to VIII, which represent the family Iphiopsididae, are characterized by a regressive autapomorphy: loss of seta av2 on tibia I (62) with the exception of *Julolaelaps*, *Gecarcinolaelaps*, and *Iphiopsis*. Group VI represents only one genus, *Scissuralaelaps*, defined by four synapomorphies: 3, 12-13, 48-49 and 61.

Groups VII and VIII share two synapomorphies: hypostomal process reduced (11), additional setae (px) between J and Z series present (32); and three apomorphies: setae s6 (22) and r6 (23) not on the shield, and loss of seta pl2 on genu IV (58), a state which also has evolved independently in the Hypoaspidae.

Group VII is defined by the loss of setae hyp1 or hyp 3 on the gnathosoma (5), which have also evolved independently in group V of the Hypoaspidae, and a short or absent peritreme

(34). Finally, Group VIII is characterized by a deutosternum with less than 6-7 rows of denticles.

When some taxa associate of mammals (*Laelaps*, *Haemogamasus*, *Myonyssus*, *Alphalaelaps*, *Echinonyssus*, *Mesolaelaps* and *Androlaelaps fahrenheitsi*) were included in the analyses, the tree length went up and the consistency index decreased, indicating a higher number of homoplasies. None of the characters used in this study can be used to define one group of taxa associated with mammals even though they always come together in the tree. This group of laelapids should be recognized as different taxonomic ranks. They have been temporarily included in different subfamilies (i.e., *Haemogamasinae*, *Myonyssinae*, *Alphalaelapinae*, *Hirstionyssinae*, *Laelapinae* and *Mesolaelapinae*) following Evans and Till, 1966, and Radovsky, 1985. The species *Androlaelaps fahrenheitsi* should be placed in a separate genus (*Haemolaelaps*), closely related with those laelapines associated with vertebrates and leaving the genus *Androlaelaps* for species which are predators or occasionally associated with nests of vertebrates.

Evans and Till (1966) studying the free-living, paraphagic and ectoparasitic British "Derma-

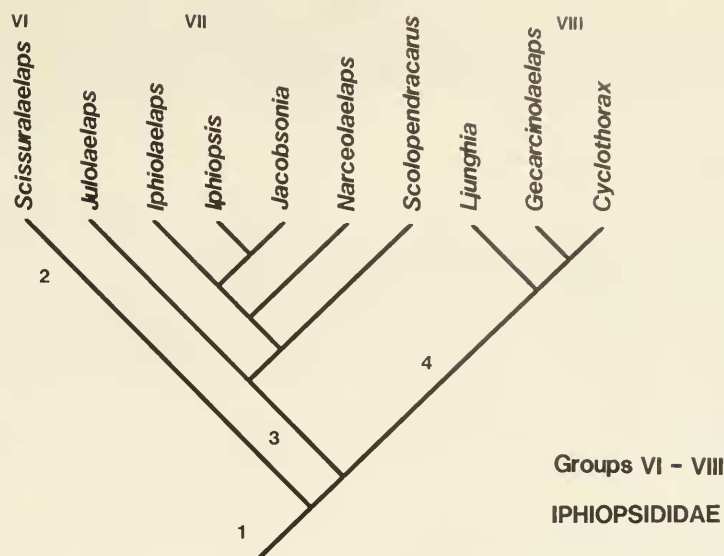


FIG. 7. Groups VI, VII and VIII: Family Iphiospididae. Group VI: Scissuralaelapinae, new subfamily. Numbers on figure refer to stems. Apomorphic characters are listed for each stem.

STEM 1: 62; STEM 2: 3, 61; STEM 3: 11, 22, 23, 32; STEM 4: 5; STEM 5: 6, 7.

nyssidae" recognized eight subfamilies: Dermanyssinae, Haemogamasinae, Pseudolaelapinae (*Pseudolaelaps*), Myonyssinae (*Myonyssus*), Melittiphidinae (*Melittiphis*), Laelapinae, Hirstionyssinae and Macronyssinae. They included within Laelapinae all the free-living laelapids and the species belonging to the following genera: *Laelaps*, *Androlaelaps*, *Pneumolaelaps*, *Gymnolaelaps*, *Holostaspis* and *Laelaspis*. They indicated that *Pseudolaelaps* and *Melittiphis* show greater affinities with Laelapinae than with any other subfamily. In this study, *Pseudolaelaps* always showed greater affinities with the outgroup than with any Laelapidae. It shares more symplesiomorphies than synapomorphic characters with Laelapidae and it presents a trispinate tectum, and hypotrichy of the idiosoma and appendages. Therefore, it is suggested that *Pseudolaelaps* should be removed from Laelapidae. Further studies are needed to determine its correct family placement. *Melittiphis*, as well as

other laelapid mites associates of Hymenoptera and Isoptera, has been included in the subfamily Melittiphidinae

Karg (1979) attempted to give a phylogenetic key for the subgenera *Hypoaspis*, *Cosmolaelaps*, *Alloparasitus*, *Gaeolaelaps*, *Pneumolaelaps*, *Holostaspis* and *Laelaspis*, including as the most relevant characters: a) tectum with toothed margin or smooth = 0, 1; b) deutosternal rows polydont or oligodont = 0, 1; c) opisthonotal seta Z4 not elongated or elongated = 0, 1; d) female genital shield normal or greatly expanded = 0, 1; and e) genital shield with one pair or more than one pair of seta = 0, 1. An analysis using these characters was done and the results showed that the characters used by Karg vary so much within even each genus that they cannot be used as binary state characters. Some of Karg's characters were used in this study, but they were polarized following the additive method.

III. CLASSIFICATION

On the basis of the proposed phylogeny the following classification of the family Laelapidae is suggested.

Family Laelapidae Berlese, 1892

A. Subfamily Hypoaspidinae Vitzthum, 1940

a) Tribe Pseudoparasitini Vitzthum, 1940

- Ololaelaps* Berlese, 1903; type-species: *Hypoaspis venetus* Berlese, 1903
- Pseudoparasitus* Oudemans, 1902; type-species: *Laelaps meridionalis* Canestrini, 1882
- Gaeolaelaps* Tragardh, 1952; type-species: *Laelaps aculeifer* Canestrini, 1884
- Alloparasitus* Berlese, 1920; type-species: *Laelaps (Hypoaspis) oblongus* Halbert, 1915
- Cosmolaelaps* Berlese, 1903; type-species: *Laelaps claviger* Berlese, 1883
- Euandrolaelaps* Bregetova, 1977; type-species: *Laelaps (Androlaelaps) sardous* Berlese, 1911
- Stratiolaelaps* Berlese, 1882; type-species: *Laelaps (Iphis) miles* Berlese, 1892

b) Tribe Hypoaspidini Vitzthum, 1940

- Androlaelaps* Berlese, 1903; *A. casalis* group
- Hypoaspis* Canestrini, 1885; type-species: *Gamarus krameri* G. & R. Canestrini, 1881
- Coleolaelaps* Berlese, 1903; type-species: *Laelaps (Iphis) agrestis* Berlese, 1887
- Dyscinetonyssus* Moss & Funk, 1965; type-species: *Dyscinetonyssus hystricosus* Moss & Funk, 1965
- Blaberolaelaps* Costa, 1980; type-species: *Blaberolaelaps matthiesensis* Costa, 1980
- Gromphadorholaelaps* Till, 1969; type-species: *Gromphadorholaelaps schaefferi* Till, 1969

B. Subfamily Melittiphidinae Evans and Till, 1966

c) Tribe Laelaspini, new tribe

- Gymnolaelaps* Berlese, 1916; type-species: *Laelaps myrmecophilus* Berlese, 1892
- Holostaspis* Kolenati, 1858; type-species: *Holostaspis isotricha* Kolenati, 1858
- Laelaspis* Berlese, 1903; type-species: *Iphis astronomicus* Koch, 1889
- Myrmonyssus* Berlese, 1903; type-species: *Myrmonyssus diplogenus* Berlese, 1903
- Pneumolaelaps* Berlese, 1920; type-species: *Iphis bombicolens* Canestrini, 1885
- Hunteria* Delfinado-Baker, Baker & Flechtmann, 1984; type-species: *Hunteria brasiliensis* Delfinado-Baker, Baker & Flechtmann, 1984
- Laelaspoides* Eickwort, 1966; type-species: *Laelaspoides ordwayae* Eickwort, 1966

d) Tribe Melittiphidini Evans and Till, 1966

- Bisternalis* Hunter, 1963; type-species: *Bisternalis rettenmeyeri* Hunter, 1963
- Myrmolaelaps* Tragardh, 1906; type-species: *Myrmolaelaps equitans* Tragardh, 1906
- Neoberlesia* Berlese, 1892; type-species: *Neoberlesia equitans* Berlese, 1892
- Neohypoaspis* Delfinado, Baker & Roubik, 1983; type-species: *Neohypoaspis ampliseta* Delfinado, Baker & Roubik, 1983
- Melittiphis* Berlese, 1918; type-species: *Laelaps (Iphis) alvearius* Berlese, 1896
- Melittiphisoides* Delfinado-Baker, Baker & Flechtmann, 1984; type-species: *Melittiphisoides apiarium* Delfinado-Baker, Baker & Flechtmann, 1984

e) Tribe Varroini Delfinado and Baker, 1974

- Tropilaelaps* Delfinado, 1961; type-species: *Tropilaelaps clareae* Delfinado, 1961
- Urozercon* Berlese, 1901; type-species: *Urozercon paradoxus* Berlese, 1901
- Stevelus* Hunter, 1963; type-species: *Stevelus amicus* Hunter, 1963
- Euvarroa* Delfinado & Baker, 1974; type-species: *Euvarroa sinhai* Delfinado & Baker, 1974
- Varroa* Oudemans, 1904; type-species: *Varroa jacobsoni* Oudemans, 1904
- Dinogamasus* Kramer, 1898; type-species: *Dinogamasus crassipes* Kramer, 1898

C. Subfamily Haemogamasinae Oudemans, 1926

Eulaelaps, Brevisterna, Ischyropoda, Acanthochela, Haemogamasus

D. Subfamily Alphalaelapinae Tipton, 1960

Alphalaelaps

E. Subfamily Laelapinae Berlese, 1992

Aetholaelaps, Cavilaelaps, Chrysochlorolaelaps, Domrownyssus, Gigantolaelaps, Gnatholaelaps, Hymenolaelaps, Hyperlaelaps, Laelaps, Liponysella, Nakhoda, Longolaelaps, Mysolaelaps, Neolaelaps, Neoparalaelaps, Notolaelaps, Ondatralaelaps, Oryctolaelaps, Permelaelaps, Radfordilaelaps, Rhyzolaelaps, Sinolaelaps, Steptolaelaps, Tricholaelaps, Tylolaelaps, Tur

F. Subfamily Myonyssinae Bregetova, 1956

Myonyssus

G. Subfamily Hirstionyssinae Evans and Till, 1960

Echinonyssus, Ancoranyssus, Patrinyssus, Thadeua, Trichosuroaelaps

H. Subfamily Mesolaelapinae Tenorio and Radovsky, 1974

Mesolaelaps, Rhodacantha

Note: Subfamilies C to H were not analyzed in this study. The list of genera in these subfamilies was taken from Radovsky, 1985.

Family Iphiopsididae Kramer, 1886

A. Subfamily Scissuralaelapinae new subfamily

Scissuralaelaps Womersley, 1945; type-species: *Scissuralaelaps novaguinea* Womersley, 1945

B. Subfamily Iphiopsidinae Kramer, 1886

a) Tribe Iphiopsidini Kramer, 1886

Julolaelaps Berlese, 1916; type-species: *Julolaelaps dispar* Berlese, 1916

Iphiolaelaps Womersley, 1956; type-species: *Iphiolaelaps myriapoda* Womersley, 1956

Iphiopsis Berlese, 1882; type-species: *Iphis mirabilis* Berlese, 1882

Jacobsonia Berlese, 1910; type-species: *Iphiopsis (Greeniella) submollis* Berlese, 1910

Narceolaelaps Kethley, 1978; type-species: *Narceolaelaps annularis* Kethley, 1978

Scolopendracarus Evans, 1955; type-species: *Scolopendracarus brevipilis* Evans, 1955

b) Tribe Gecarcinolaelapini, new tribe

Ljunghia Oudemans, 1932; type-species: *Ljunghia selenocosmiae* Oudemans, 1932

Cyclothorax von Frauenfeld, 1868 type-species: *Cyclothorax carcinicola* von Frauenfeld, 1868

Gecarcinolaelaps n. gen. Type-species: *Gecarcinolaelaps cancer* (Pearse, 1929) n. comb.

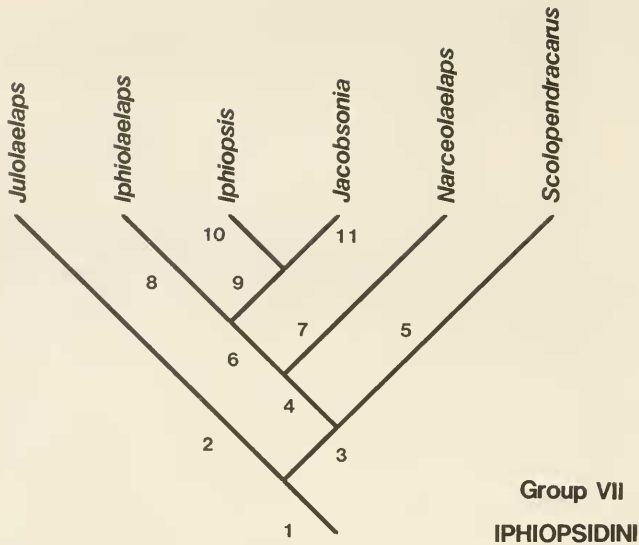


FIG. 8. Group VII: Iphiopsini. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.
STEM 1: 5; STEM 2: 29; STEM 3: 46, 47, 49, 50, 52, 56, 60, 61, 72; STEM 4: 48, 59, 63, 66; STEM 5: 9, 10, 24, 25, 26, 28, 53, 54, 57; STEM 6: 51, 53, 54, 55, 64, 67, 70; STEM 7: 9, 27, 65; STEM 8: 18, 35; STEM 9: 13, 29, 57, 65; STEM 10: —; STEM 11: 21, 24, 35, 37.

The free-living laelapid mites, Group I, are ranked at the tribe level. These genera are plesiomorphic in many character states relative to the other laelapid-type mites. For example, a denticulate tectum, four pairs of subcapitular setae, normal and bifid tritosternum, normal leg chaetotactic pattern, etc., characters which are also present in the Ologamasidae and Leptolaelapidae, and may well represent the plesiomorphic states for the laelapid mites.

The name Hypoaspidae Vitzthum has priority over other available family group names for the subfamily proposed here to include groups I (Pseudoparasitini) and II (Hypoaspidini). These two groups constitute a well-defined monophyletic lineage representing the sister group of the other laelapid mites.

Since the genera of groups III to V are members of a simple well-defined monophyletic group, they are considered as one subfamily, Melittiphidinae. The name Melittiphidinae has priority over the family name Varroidae for the subfamily proposed here.

Each group (III, IV and V) within the subfamily Melittiphidinae are assigned tribal rank: group III represents the tribe Laelaspini, new tribe, to include genera associated with Formicidae and Apidae; group IV is tribe Melittiphidini which includes six genera associated with Hymenoptera; and group V represents tribe Varroini which are associates of honey-bees, carpenter bees, bumblebees and Isoptera.

The species in the subfamilies Haemogamasinae, Alphalaelapinae, Laelapinae, Myonyssinae, Hirstionyssinae and Mesolaelapinae, all associates of mammals, were not analyzed in detail here. However, when some of these genera were included in the analyses they always diverged from the Hypoaspidae. Therefore, their subfamily rank is retained until more analyses are done. The mammal-associated laelapid mites and the Hypoaspidae are characterized by one synapomorphic character: loss of seta pv1 on genu IV, which is a regressive apomorphy.

The groups VI, VII and VIII represent a new family group: Iphiopsidae. Previous allocation of

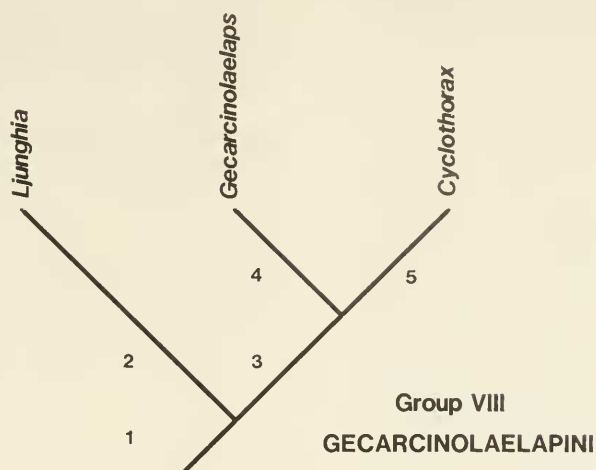


FIG. 9. Group VIII: Gecarcinolaelapini, new tribe. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 6, 7; STEM 2: 18, 21, 25, 28; STEM 3: 48, 57, 60, 61; STEM 4: 10, 30, 41, 52, 70; STEM 5: 12, 14, 18, 25, 26, 37, 49, 50, 63, 66.

the genera of these groups was in the subfamily Iphiopsidinae within Laelapidae (Evans, 1955). The iphiopsid mites represent a well-defined and monophyletic group that includes paraphages of Chilopoda, Diplopoda, Araneae and Crustacea.

According to the phylogenetic analyses the family Iphiopsididae Kramer present two subfamilies: Iphiopsidinae, divided into two tribes: Iphiopsidini Kramer, and Gecarcinolaelapini new tribe; and Scissuralaelapinae new subfamily.

Scissuralaelapinae (group VI) represents the sister group of the other two groups of iphiopsid mites. Iphiopsidini is a well-defined and monophyletic group which includes paraphages of Chilopoda and Diplopoda. Considering the setal losses some members of the family Iphiopsididae, *Jacobsonia* and *Iphiopsis*, are among the most regressive mesostigmatid mites known and this is the result of the retention of larval character states (paedomorphosis).

The appropriate taxonomic status of the genera (especially *Ljunghia*) temporarily included in the tribe Gecarcinolaelapini, which are associates of Crustacea and Araneae, will become apparent when new data are analyzed.

CONCLUSIONS

The phylogeny proposed for the free-living and arthropod-associated laelapid mites based on parsimony methods represents a substantial improvement in understanding the evolutionary history of the group, and gives a basis to understand the most derived groups within the cohort Dermanyssina.

Many characters of laelapid mites have yet to be analyzed phylogenetically due to the incompleteness of data and, therefore, the proposed phylogeny must be regarded as preliminary. When data on the immature stages and males, as well as life-history and habitat diversification, become available a more strongly based phylogeny of the family Laelapidae can be achieved.

Concepts of the free-living and arthropod-associated Laelapidae were reviewed in an attempt to determine the internal relationships of the members of the family. Using phylogenetic methods, PAUP and MacClade programs, a comparative study of eighty-three characters in forty-three generic taxa resulted in the construction of nine con-

sensus cladograms illustrating familial and subfamilial relationships. The *Leptolaelapidae* Karg, 1978 was used as the sister group and *Ologamasidae* Ryke, 1962 as the outgroup to the *Laelapidae*.

In the revision of the taxa included in this study, it is intended that the taxa reflect natural hierarchical groups and to be defined on the basis of synapomorphies where possible. Tree length and consistency index were sometimes sacrificed to obtain the most definable groups of laelapid mites.

The *Laelapidae* was redefined to include eight subfamilies: *Hypoaspidae* Vitzthum, 1940; *Melittiphinae* Evans and Till, 1966; *Haemogamasinae* Oudemans, 1926; *Alphalaelapinae* Tipton, 1960; *Laelapinae* Berlese, 1892; *Myonyssinae* Bregetova, 1956; *Hirstionyssinae* Evans and Till, 1960; and *Mesolaelapinae* Tenorio and Radovsky, 1974. The new arrangement of the free-living and arthropod-associated genera is the following: Family *Laelapidae*, with two subfamilies: a. Subfamily *Hypoaspidae*, which includes the free-living, predatory and phoretic mites on Coleoptera and Blattaria, with: Tribe *Pseudoparasitini* (*Alloparasitus*, *Cosmolaelaps*, *Euandrolaelaps*, *Gaeolaelaps*, *Ololaelaps*, *Pseudoparasitus*, *Stratiolaelaps*); Tribe *Hypoaspidini* (*Androlaelaps casalis* group, *Blaberolaelaps*, *Coleolaelaps*, *Dyscinetonyssus*, *Gromphadorholaelaps*, *Hypoaspis*); b. Subfamily *Melittiphidinae*, which includes laelapid mite associates of Hymenoptera (Apidae and Formicidae) and Isoptera, with: Tribe *Melittiphidini* (*Bisternalis*, *Myrmolaelaps*, *Neoberlesia*, *Neohypoaspis*, *Melittiphis*, *Melittiphisoides*); Tribe *Varroini* (*Dinogamasus*, *Euvarroa*, *Stevulus*, *Tropilaelaps*, *Urozercon*, *Varroa*).

The family *Iphiopsididae*, which includes dermanyssoid mite associates of Chilopoda, Diplopoda, Araneae and Crustacea is divided into two subfamilies: a. Subfamily *Scissuralaelapinae*, new subfamily (*Scissuralaelaps*); b. Subfamily *Iphiopsidinae* with: Tribe *Iphiopsidini* (*Iphiolaelaps*, *Iphiopsis*, *Jacobsonia*, *Julolaelaps*, *Narceolaelaps*, *Scolopendracarus*); and Tribe *Gecarcinolaelapini*, new tribe (*Cyclothorax*, *Gecarcinolaelaps*, *Ljunghia*).

The genus *Urozercon* is included for the first time in the family *Laelapidae*; and the new genus *Gecarcinolaelaps* is established in *Iphiopsididae*. The prior ranking of *Euvarroa* and *Varroa* as the family *Varroidae* Delfinado and Baker, 1974 is refuted.

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